Late Ediacaran occurrences of the organic-walled microfossils *Granomarginata* and flask-shaped *Lagoenaforma collaris* gen. et sp. nov.

Heda Agić1, Anette E.S. Högström2, Sören Jensen3, Jan Ove R. Ebbestad4, Patricia Vickers-Rich5,6, Michael Hall5, Jack J. Matthews7, Guido Meinhold8,9, Magne Høyberget10 and Wendy L. Taylor11

1Department of Earth Science, University of California Santa Barbara, Santa Barbara, CA, USA; 2Arctic University Museum of Norway, UiT – The Arctic University of Norway, Tromsø, Norway; 3Área de Paleontología, Universidad de Extremadura, Badajoz, Spain; 4Museum of Evolution, Uppsala University, Uppsala, Sweden; 5School of Earth, Atmospheric and Environment, Monash University, Clayton, Victoria, Australia; 6Department of Chemistry and Biotechnology, School of Science, Swinburne University of Technology, Hawthorn, Victoria, Australia; 7Oxford University Museum of Natural History, Oxford, UK; 8Institut für Geologie, TU Bergakademie Freiberg, Freiberg, Germany; 9Department of Sedimentology and Environmental Geology, University of Göttingen, Göttingen, Germany; 10Renesseveien 14, Mandal, Norway and 11Department of Geological Sciences, University of Cape Town, Rondebosch, South Africa

**Abstract**

New occurrences of flask-shaped and envelope-bearing microfossils, including the predominantly Cambrian taxon *Granomarginata*, are reported from new localities, as well as from earlier in time (Ediacaran) than previously known. The stratigraphic range of *Granomarginata* extends into the Cambrian System, where it had a cosmopolitan distribution. This newly reported Ediacaran record includes areas from Norway (Baltica), Newfoundland ( Avalonia) and Namibia (adjacent to the Kalahari Craton), and puts the oldest global occurrence of *Granomarginata* in the Indredvela Member (< 563 Ma) of the Ståhpogieddi Formation on the Digermuken Peninsula, Arctic Norway. Although *Granomarginata* is rare within the assemblage, these new occurrences together with previously reported occurrences from India and Poland, suggest a potentially widespread palaeogeographic distribution of *Granomarginata* through the middle–late Ediacaran interval. A new flask-shaped microfossil *Lagoenaforma collaris* gen. et sp. nov. is also reported in horizons containing *Granomarginata* from the Ståhpogieddi Formation in Norway and the Dabis Formation in Namibia, and flask-shaped fossils are also found in the Gibbett Hill Formation in Newfoundland. The *Granomarginata–Lagoenaforma* association, in addition to a low-diversity organic-walled microfossil assemblage, occurs in the strata postdating the Shuram carbon isotope excursion, and may eventually be of use in terminal Ediacaran biostratigraphy. These older occurrences of *Granomarginata* add to a growing record of body fossil taxa spanning the Ediacaran–Cambrian boundary.

1. **Introduction**

The Ediacaran Period (635–538.8 Ma) is the most recently defined and longest geological period (Knoll et al. 2006; Xiao et al. 2016), and it encompasses a time of significant environmental and biotic changes (Droser et al. 2017; Darroch et al. 2018; Wood et al. 2019). Efforts to subdivide and better constrain timing of these events include carbon isotope chronostratigraphy and biostratigraphy based on faunas of Ediacara-type macrofossils, microfossils (acanthomorphic acritarchs) and trace fossils (Grey, 2005; Jensen et al. 2006; Willman & Moczydłowska, 2011; Narbonne et al. 2012; Macdonald et al. 2013; Xiao et al. 2016; Rooney et al. 2020; Darroch et al. 2021), although much work remains. These efforts face challenges compared with Palaeozoic or younger strata due to taphonomic bias, a relatively low diversity of fossil organisms and a high degree of endemism (cf. Droser et al. 2017; Muscente et al. 2019). Use of trace fossils and biomineraling taxa as biostratigraphic indicators is mostly applied to upper Ediacaran strata (e.g. Jensen et al. 2006; Tarhan et al. 2020; Darroch et al. 2021; Chai et al. 2021). However, through integration of diverse types of palaeontological and palaeoenvironmental records, a better understanding of the event timeline is emerging, and the community is moving towards a subdivision of the Ediacaran Period at stage level and a better understanding of the sequence of evolutionary events (Xiao et al. 2016; Shahkarami et al. 2020).

Organic-walled microfossils (OWM; including acritarchs) are used as a proxy for diversity of eukaryotic microbiota and are also one of the biostratigraphic tools for constraining the age of Ediacaran successions (e.g. Grey, 2005; Xiao et al. 2016). Acritarchs are a polyphyletic group of...
mostly single-celled organisms, likely representing a variety of microscopic eukaryotes. They are composed of acid-insoluble organic matter and commonly preserved as compressed carbonaceous vesicles in fine-grained siliciclastics, or by permineralization in cherts or phosphorites. Historically, three assemblages of OWM have been identified during the Ediacaran Period (Grey et al. 2003; Grey, 2005); Ediacaran leiosphere palynoflora (ELP); Ediacaran complex acanthomorph palynoflora (ECAP, also referred to as Doushantuo–Pertattaka acritarchs (DPA)) dominated by large process-bearing forms; and late Ediacaran leiosphere palynoflora (LELP), composed mainly of sphaeromorphic OWM. Eukaryotic microfossils were especially diverse during early Ediacaran time as exemplified by taxonomically rich assemblages from Australia (Zang & Walter, 1992; Grey, 2005; Willman & Moczydłowska, 2011), China (Xiao et al. 2014; Liu & Moczydłowska, 2019), the East European Platform (Vorob’eva et al. 2009), Siberia (Sergeev et al. 2011; Moczydłowska & Nagovitsin, 2012), India (Prasad et al. 2010; Joshi & Tiwari, 2016) and Laurentia (Willman et al. 2020). They have been used in biostatigraphic endeavours to correlate Ediacaran strata (e.g. Grey, 2005; Xiao et al. 2016), usually antedating the widespread occurrence of the macroscopic Ediacara-type biota (see Xiao et al. 2016). In contrast, the ELP and LELP assemblages are generally depauperate, mostly consisting of simple leiosphaerid acritarchs that possess few distinguishing characters, or other non-diagnostic taxa with very long stratigraphic ranges (e.g. Grey, 2005; Chiglino et al. 2015; Kolesnikov et al. 2015; Lehn et al. 2019). Exceptions were discovered recently; some acanthomorphic (process-bearing) OWM persisted to the latest Ediacaran of Mongolia (Anderson et al. 2019) and Russia (Grazhdankin et al. 2020). Such assemblages remain rare towards the end of the Ediacaran Period and could have been restricted to specific environments where acanthomorphs thrived or were able to be preserved. More upper Ediacaran strata need to be examined for microfossils in detail, and their utility in a more refined stratigraphic subdivision of the later Ediacaran Period (the upper series) is in progress.

Only a handful of body-fossil taxa span the Ediacaran–Cambrian boundary (Slater et al. 2020). Recent studies have shown that several fossil groups persisted through this interval, including skeletal metazoan taxa (cloudinids), small carbonaceous fossils (SCF) and organic problematica (Moczydłowska et al. 2015; Yang et al. 2016; Zhu et al. 2017; Slater et al. 2020). Microfossils in this study show a similar trend; we found the predominantly Cambrian taxon Granomarginata Naumova (1960) deeper in time, within Ediacaran strata representing a shallow-water to distal shelf-marine environment in Arctic Norway, and nearshore shallow-water setting in Namibia and Newfoundland (Figs 1–4). In addition to Granomarginata previously reported from India (Kumar & Maithy, 2008; Prasad et al. 2010) and Poland (Jachowicz-Zdanowska, 2011), our new records suggest a geographically widespread distribution of Granomarginata by late Ediacaran time. We further report additional diagnostic OWM co-occurring with Granomarginata, including the new flask-shaped taxon Lagoenaforma collaris gen. et sp. nov.

2. Methods

Microfossils were isolated from the rock matrix utilizing a palynological extraction procedure (Grey, 1999) that includes maceration in 40% hydrofluoric acid (HF) to dissolve silicates, and boiling of the residue in 30% hydrochloric acid (HCl) to remove fluorides. Calcareous fine sandstone samples were first macerated in HCl for > 24 hours to remove carbonates. Residue was filtered through 10 μm mesh and used to prepare smear mounts for a light microscopy overview. Microfossils were observed and imaged with a Zeiss Axioskop 40 transmitted light microscope with Q Imaging camera. All illustrated specimens from the Digerumlen Peninsula will be deposited in the palaeontological collections (TSGF) of the Arctic University Museum of Norway, Tromsø, and specimens from Namibia at the Geological Survey of Namibia, Windhoek. To evaluate abundance and diversity, all microfossils were counted on one slide per sample.

Fossiliferous samples were collected from middle–upper Ediacaran strata in three distinct areas: Arctic Norway, Namibia and Newfoundland. Granomarginata was recovered from a new locality as well as in strata older than previously reported, which prompted a comparison of the OWM assemblages between these areas.

3. Geological setting

3.a. Arctic Norway

Samples from Arctic Norway were collected during the 2016 and 2018 field expeditions of the Digerumlen Early Life Research Group (DELRG). The Digerumlen Peninsula in the Finnmark region of mainland Arctic Norway hosts an approximately 3-km-thick succession of mainly siliciclastic sedimentary rocks of Cryogenian–Ordovician age (e.g. Högström et al. 2013; Figs 1a, b, 2a, 3a). The base of the Vestertana Group contains glaciogenic diamictites of the Smallfjorden and Mortensnes formations that have been linked to the Marinoan and Gaskiers glacial intervals, respectively (Halverson et al. 2005). These sequences bracket the siliciclastic shallow-marine to basinal, non-glacial Nybrøg Formation. Organic-walled microfossil taxa characteristic of the early Ediacaran Period (ECAP/DPA), as well as organically preserved remnants of multicellular tissue, have been documented in the upper part of the Nybrøg Formation (Agić et al. 2018, 2019). Overlying the Mortensnes diamictite is the Ståhpogieddi Formation, which starts with sandstones and shales of the Lillevannet Member, representing a transgressive interval (Banks et al. 1971; Jensen et al. 2018b). Above lies the Indreelva Member composed of mudstones, siltstones and sandstones, which hosts an assemblage of Ediacara-type macrofossils dominated by discoidal taxa (Farmer et al. 1992; Högström et al. 2013, 2017; Jensen et al. 2018b). The overlying Mannadrapselva Member consists of a basal sandstone unit, followed by two upwards-coarsening cycles of red and grey mudstone and sandstone alterations and, in the second cycle, carbonate concretions and calcareous siliciclastic beds (Meinhold et al. 2019a). The stratigraphically highest occurrence of macrofossils Palaeopascichnus and Harlaniella is c. 15 m above the carbonates, and the Ediacaran–Cambrian boundary lies close to the base of the third cycle, indicated by the occurrence of the trace fossil Treptichnus pedum (Fig. 2a; McIlroy & Brasier, 2017; Jensen et al. 2018a, b).

Fossiliferous samples discussed here were collected from shales and siltstones in the basal part of Indreelva Member from Árasulluokta Cove (Fig. 1a, b). Samples D16-HA-80 (70° 34.165’ N, 28° 07.224’ E) and D18-HA-20 (70° 34.174’ N, 28° 07.204’ E, just above a bed with discoidal fossils), were collected 3 m and c. 10 m above the lowest occurrence of palaeopascichnids (cf. Jensen et al. 2018b). Sample D16-HA-53 was recovered 2 m below the earliest aspidellomorphs in the Ståhpogieddi section, 6 m above the Lillevannet–Indreelva transitional beds (70° 32.534’ N, 28° 00.929’ E). The sample from the Mannadrapselva Member third
Fig. 1. (Colour online) Localities of sample collections and outcrops with occurrences of *Granomarginata* and *Lagoenaforma* gen. nov. (a) Basal part of the Indreelva Member of the Stáhpogieddi Formation, Vestertana Group in coastal outcrops in northern portion of Árasulluokta Cove, southeastern shore of the Digermulen Peninsula in Norway. (b) Shales and siltstones of the Indreelva Member above the occurrence of macrofossil *Palaeopascichnus*. (c) Basal Nama Group strata on Farm Pockenbank in the Witputs sub-basin in Namibia. (d) Fine arenite of the Mara Member, Dabis Formation, Nama Group exposed on Farm Pockenbank. (e) Gibbett Hill Formation, exposed at the ‘Brasier Shale’ outcrop on the northern shore of Ferryland Head, eastern coast of the Avalon Peninsula, Newfoundland. This locality was named in honour of Professor Martin Brasier who spent many field excursions studying this outcrop. (f) Enhanced view of the Brasier Shale in the upper Gibbett Hill Formation.
cycle at the Manndrapselva River section (D16-HA-77, 70° 34.575' N, 28° 06.847' E) was collected immediately above the quartzite marking the top of the second cycle.

3.b. Namibia

Fossiliferous samples from Namibia were collected from the Dabis Formation during the field workshop on the Ediacaran Nama Group of southern Namibia, part of the IGCP 587 programme (Xiao et al. 2017) on Farm Pockenbank (Figs 1c, d, 2b, 3b). The Nama Group contains c. 3 km of fluvial to marine siliciclastics and carbonates, representing a tidal to below-wave-base environment of a foreland basin (Germs et al. 1986; Germs & Gresse, 1991). It occurs in a northern Zaris sub-basin and a southern Witputz sub-basin, separated by the Osis Ridge (Germs, 1983). The lower part of the Nama, the Kuibis Subgroup, consists of 200 m of mature siliciclastics and carbonates, and is subdivided into the Dabis and Zaris formations (Germs, 1983; Saylor et al. 1995). In the Pockenbank area (Witputz sub-basin), the lowermost Kanies Member of the Dabis Formation contains predominantly arkosic sandstones with ripples and desiccation cracks indicative of shallow, fluvial environments (Germs, 1983; Saylor et al. 1995). The Mara Member overlies the transgressively eroded top of the Kanies Member, and contains alternating fine-grained siliciclastics and limestones with microbialites and evaporites within a shallowing-upwards sequence (Germs, 1972; 1983; Saylor et al. 1995). Above the Mara Member are the Kliphoek and Aar members that consist of cross-stratified coarse sandstones and carbonates (Germs, 1983; Saylor et al. 1995; Hall et al. 2013). Saylor et al. (1995) interpreted the Dabis Formation strata as two transgressive sequences. Some of the oldest examples of the youngest Ediacaran evolutionary assemblage – the Nama assemblage – occur in the Kliphoek/Aar members (e.g. Germs, 1983; Narbonne et al. 1997; Vickers-Rich et al. 2013; Maloney et al. 2020).

Carbonates (micrite phases) in the Mara Member (Arasab section) preserve a negative $\delta^{13}$C excursion from $-6.22$‰ to $-0.22$‰, previously correlated with the recovery from the global Shuram–Wonoka anomaly (Kaufmann et al. 1991; Saylor et al. 1995, 1998; Grotzinger et al. 1995; Hall et al. 2013; Wood et al. 2015). The excursion is not fully manifested at the locality where the microfossils were collected (cf. Vickers-Rich et al. 2016). Sandstones of the overlying Kliphoek and Aar members include fossils in offshore-shoreface settings, characteristic environments inhabited by the late Ediacaran Nama assemblage including such taxa as Ernietta, Pteridinium and Rangea, as well as macroscopic bacterial colonies Nemiana (Narbonne et al. 1997, 2012;
Vickers-Rich et al. (2013). These macrofossiliferous strata span the late Ediacaran Period: an ash bed in the Kuibis Subgroup yielded a U–Pb age of 548.8 ± 1 Ma (Grotzinger et al. 1995), and ash beds from the Spitskop Member of the overlying Urusis Formation yielded ages of 538.99 ± 0.21 Ma in the most recent study using U–Pb chemical abrasion–isotope dilution–thermal ionization imaging spectrometry (CA-ID-TIMS) dating technique (Linnemann et al. 2019).

Collection for a pilot microfossil survey was carried out from the lower Mara Member, Nama Group on Farm Pockenbank, at the Quiver section (see Vickers-Rich et al. 2016): N16-HA-P2 c. 9 m above the base of the Mara Member (27° 08.619' S, 16° 26.803' E), and N16-HA-P3 immediately above a grey limestone package. These strata are overlain by grey and pink dolomite, and dark limestone at the top.

3.c. Newfoundland, Canada

The microfossiliferous Gibbett Hill Formation of the Signal Hill Group is exposed on the eastern Avalon Peninsula, Newfoundland, Canada (Sala Toledo, 2004; Hofmann et al. 2008). The Signal Hill Group overlies the fossiliferous strata of
the Conception and St John’s groups, which contain some of the oldest Ediacara-type macrofossils, that is, the Avalon assemblage (Fig. 2c; Misra, 1969; Narbonne in Fedonkin et al. 2007; Liu et al. 2015; Matthews et al. 2021). Temporal constraints in the upper part of this succession are generally scarce, but the Conception Group contains a glacial diamictite (Gaskiers Formation) dated between 580.90 ± 0.40 and 579.88 ± 0.44 Ma using CA-ID-TIMS U–Pb analyses on zircon grains (Pu et al. 2016), and the rangeomorphs from the Fermeuse Formation in the upper St John’s Group, have a maximum age of 564.13 ± 0.65 Ma (Matthews et al. 2021). A tuffite sample from the lower Fermeuse Formation yielded zircon U–Pb dates from 563.67–569.01 Ma (Matthews et al. 2021).

The overlying Signal Hill Group contains c. 1500 m of mudstones, fine-grained sandstones and ash beds (Sala Toledo, 2004). Its oldest unit is the Cappahayden Formation, containing laminated grey siltstones. It is overlain by the Gibbett Hill Formation consisting of 760 m of green-grey sandstone, mudstone and black shales (Sala Toledo, 2004) and deposited in a shallow-marine environment.

Rare OWM dominated by sphaeromorphs were previously reported from siliciclastics of the Drook, Mall Bay, Fermeuse and Renews Head formations in the St John’s Group (Hofmann et al. 1979; O’Brien & King, 2004), and the Cappahayden Formation (underlying the Gibbett Hill Formation) in the Signal Hill Group (Hofmann et al. 1979). The microfossils in this study derive from a single sample of the ‘Brasier Shale’ outcrop in the Gibbett Hill Formation, near Ferryland, Avalon Peninsula, Newfoundland (Fig. 1e–f).

4. Results

A flask-shaped OWM Lagoenaforma gen. nov. (Fig. 5) was found in several upper Ediacaran units. This taxon frequently occurs with rare Granomarginata squamacea and G. prima, which are typically early Cambrian taxa. This new material, along with previous reports (Fig. 4, Table 1), extend the distribution of Granomarginata back in time into the late Ediacaran Period. These OWM also co-occur with leiosphaerids and carbonaceous problematica (Fig. 6).
4.a. Ediacaran Indreelva Member, Ståhpgieddi Formation, Digermulen Peninsula, Norway

Out of 13 analysed samples from the Indreelva Member, 10 were barren or had very low organic content, and the rest yielded moderately well preserved OWM. These include: *Granomarginata prima*, *G. squamacea*, *Leiosphaeridia crassa*, *L. jacutica*, a tapering annulated microfossil, a lobate acritarch, fragmented SCF and aggregates of cells *Symplassosphaeridium* sp. A new type of flask-shaped OWM is described: *Lagoenaforma collaris* gen. et sp. nov. (Fig. 5a). Fragmented remains of filamentous prokaryotes and parts of rare larger SCF, as well as often torn membranous extensions of *Granomarginata*, are likely not a result of destructive processing because a low-manipulation acid maceration method was applied; this indicates either degradation within the sediment or transport. Leiosphaerids are the most common component of the Indreelva OWM assemblage (> 80%, Fig. 6a, b, d). There are few *Granomarginata* specimens; it is therefore rarer when compared with its abundance in the Cambrian strata (e.g. 3–10 counts, see Palacios et al. 2020). OWM are generally scarce in the strata examined here.

The first record of *G. squamacea* and *L. collaris* in the Indreelva Member occurs in a laminated mudrock 3 m above the level hosting palaeopascichnids, and c. 10 m above the transitional beds of the Lillevannet Member (Figs 2a, 3a). Microfossils also occur c. 6 m below the first discoidal Ediacara-type macrofossils in the Indreelva Member in the Ståhpgieddi type section. Mudrock samples below the *Palaeopascichnus* horizon in the Árasulluokta Cove were devoid of microfossils apart from rare leiosphaerid fragments. This is likely not preservational bias because at least some OWM (*leiosphaerids*) are present. *Granomarginata* makes up 4% and *L. collaris* 7.5% of the Indreelva assemblage. Overall filaments and organic problematica represent nearly 10% of the assemblage. Samples from the upper part of the Indreelva Member did not yield any microfossils. Distinct OWM are not commonly found very close to the beds containing Ediacara-type biota (Grey in Fedonkin et al. 2007). Although microfossils in the Indreelva Member are rare and occur sporadically, these results from the Digermulen Peninsula represent a rare distribution of acritarchs and Ediacaran macrofossils within a few metres of each other.
4.b. Ediacaran–Cambrian Mannndrapselva Member, Stãhpogiðdi Formation, Digermulen Peninsula, Norway

Granomarginata was previously documented higher up in the stratigraphy on the Digermulen Peninsula, in association with leiosphaerids in the third cycle of the Mannndrapselva Member of the Stãhpogiðdi Formation, correlated with the basal Terreneuvian (Hõgström et al. 2013), as well as in the Cambrian Series 2 to 5 Mialoligian Duklábagáisi Formation further up in the stratigraphy (Palacios et al. 2020). Only two samples (one fossiliferous) from the Mannndrapselva Member below the Ediacaran–Cambrian boundary were analysed here, but no Granomarginata was recovered. Instead, these strata contain organic problematica such as a neck-bearing microfossil (Fig. 5d), as well as fragments of leiosphaerids, bacterial filaments and SCF. Palacios et al. (2017) observed lobate SCF problematica upsection in the third cycle similar to microfossils from the Gibbett Hill Formation on Newfoundland (Fig. 6c).

4.c. Mara Member assemblage, Dabis Formation, Nama Group, Farm Pockenbank, Namibia

Organic-walled microfossils recovered from the Mara Member of the Nama Group on Farm Pockenbank occur in fine sandstones/silts interbedded with limestones, deposited in a shallow-marine environment. Taxa include: Granomarginata squamacea, Lagoenaforma collaris gen. et sp. nov., Leiosphaeridia crassa, Simia annulare (Fig. 6f), Bavinedella sp. (Fig. 6h), Symplasosphaeridium sp. and vesicle fragments of smooth-walled microfossils or possible SCF (Fig. 6i). Fragments of broad filaments are rare, but similar to material identified as Vendotaenia sp. from the Kuibis Subgroup by Germs et al. (1986). The newly reported microfossils here occur below strata containing possible first occurrence of cloudinids (following an unillustrated report of Cloudina by Germs, 1972a; cf. Wood et al. 2015), and they are uncomformably overlain by the Kliphoek and Aar members, which contain the Ediacara-type macrofossils Ernietta (Pflug, 1966; Elliot et al. 2016), Pteridinium (Gürich, 1930) and Rangea (Narbonne et al. 1997; Vickers-Rich et al. 2013) characteristic of the late Ediacaran Nama assemblage (Narbonne et al. 1997).

OWM from the weathered sediments of the Mara Member are slightly lighter in colour than the specimens from Newfoundland and Arctic Norway (thermal alteration index (TAI) = 3–4 sensu Hayes et al. 1983), which indicates a lower degree of thermal alteration. Leiosphaerids make up the bulk of the OWM assemblage in the Mara Member (c. 80 % of the overall microfossil abundance). Cell aggregates Symplasosphaeridium are the next most common component. Granomarginata represents 3.5% and L. collaris 6% of the assemblage. This preliminary record of Ediacaran OWM from Namibia, despite being of low diversity, is encouraging future explorations of the late Ediacaran microfossil record hosted in the Nama Group.

4.d. Gibbett Hill Formation microfossils, Signal Hill Group, Avalon Peninsula, Newfoundland, Canada

The Gibbett Hill Formation contains rare and poorly to moderately preserved OWM. The most common component are fragments of prokaryotic filaments and leiosphaerids. As a low-manipulation acid maceration method was used, the fragmentation is likely not a result of palynological processing and could instead indicate transport. Additional microfossils include prokaryotic clusters of cells Symplasosphaeridium sp., a small carbonaceous problematicum with lateral protrusions (Unnamed Form B, Fig. 6c), a fragment of a single-cell microfossil with a spongy envelope – likely Granomarginata prima (Fig. 6i) – and a dark flask-like microfossil with an elongate neck-like structure Lagoenaforma sp. (Fig. 5e). The dark colour of the Gibbett Hill OWM indicates high thermal alteration of the organic matter. Only a single specimen of a poorly preserved Granomarginata has been recovered. However, due to the presence of the late Ediacaran organic problematica (Fig. 6c) and L. collaris, which co-occur with Granomarginata in the Ediacaran strata of Norway and Namibia, the identification of envelope-bearing microfossil from Gibbett Hill as Granomarginata is plausible. These microfossils occur hundreds of metres above the fossiliferous successions hosting some of the oldest assemblage of Ediacaran macrofossils (cf. Hofmann et al. 2008; Liu et al. 2015; Matthews et al. 2021), consistent with a broadly late Ediacaran age of the Gibbett Hill Formation.

5. Discussion

5.a. Ediacaran Granomarginata

The lower Ediacaran strata accommodate a rich and diverse record of organically preserved microfossils of biostratigraphic importance (e.g. Zang. 1988; Grey, 2005; Vorob’eva et al. 2009; Sergeev et al. 2011; Willman & Moczydłowska, 2011). On the contrary, however, the strata postdating localized short-lived glaciations, the Shuram negative carbon isotope excursion (CIE) and the first appearance of the macroscopic Ediacara-type biota are generally depauperate of microfossils, with little distinctive morphologies. The strata bearing Ediacaran macrofossils rarely contain acritarchs, mainly leiosphaerids and prokaryotes (cf. Hofmann et al. 1979; Grey, 2005; Leonov & Ragozina, 2007) in lower abundance than in older, pre-Gaskiers or pre-Shuram strata. This pattern is observed on the Digermulen Peninsula where the lower Ediacaran Nyborg Formation contains acanthomorphs (Agić et al. 2018), whereas the strata above in the Stãhpogiðdi Formation are mostly barren and relatively depauperate until Cambrian time. OWM assemblages of low diversity, with few eukaryotic forms, have also been reported from Argentina, Australia, Brazil, East European Platform, Namibia and Siberia (Germs et al. 1986; Gaucher et al. 2003; Grey, 2005; Leonov & Ragozina, 2007; Chiglino et al. 2015; Kolesnikov et al. 2015; Ragozina et al. 2016; Arroyu et al. 2019; Arvestål & Willman, 2020). Late Ediacaran acanthomorphic acritarchs were found in Mongolia (Anderson et al. 2019) and in a drillcore from Siberia (Grazhdankin et al. 2020), but these occurrences are exceptions among the generally low-diversity late Ediacaran OWM assemblages.

The organic-walled microfossil genus Granomarginata is one of the more distinguishable OWM taxa of the Terreneuvian epoch, known from units in China, Canada, the East European Platform, Finland, India, Norway, Siberia, and Spain (Moczydłowska, 1991, 2011; Palacios & Moczydłowska, 1998; Kumar & Maithy, 2008; Yin et al. 2009; Palacios et al. 2018, 2020; Slater & Willman, 2019), and was also reported from the uppermost Ediacaran strata of India (Prasad et al. 2010) and Poland (Gunia, 1990; Jacobowski-Zdanowska, 2011). It is a common component of the Granomarginata prima Zone of the East European Platform (EEP) (Jankauskas & Lendzion, 1992), the Granomarginata Zone in Newfoundland (Palacios et al. 2018), and rare to common in abundance in Skiagia-bearing zones (e.g. Palacios et al. 2018, 2020) that characterize the latest Terreneuvian and Cambrian

https://doi.org/10.1017/S0016756821001096 Published online by Cambridge University Press
Late Ediacaran occurrences of the organic-walled microfossils

Fig. 6. (Colour online) Other common organic-walled microfossils co-occurring with Granomarginata and Logoenaforma gen. nov. in units of middle-late Ediacaran age, common components of the late Ediacaran leiosphaerid palynoflora (LELP, cf. Grey, 2005) as well as older Precambrian assemblages, and small carbonaceous fossils. (a) Leiosphaeridia jacutica from the upper Mara Member, Dabis Formation, Nama Group on Farm Pockenbank, Namibia. N16-HA-P2 78×19. (b) Leiosphaeridia crassa from the Mara Member, N16-HA-P2 89×11. (c) Unnamed Form B, a small carbonaceous problematicum with lateral protrusions, from the Gibbett Hill Formation, Signal Hill Group, Avalon Peninsula, Newfoundland. Brasier Shale A-1 91×11. (d) L. crassa from the Indreelva Member, Stáhpogieddi Formation, Vestertana Group in Norway. TSGf18449d, D16-HA-88 85.5×9. (e) Unnamed Form C, tapering elongated and annulated microfossil from the Indreelva Member. TSGf18450b, D16-HA-53 85×9. (f) Simia annulare from the Mara Member, Dabis Formation, Nama Group in Namibia. N16-HA-P2 77×19. (g) SCF from the Mannandrapselva Member, Stáhpogieddi Formation. TSGf18451b, D16-HA-77 88×14. (h) Bavlinella sp. from the Mara Member. N16-HA-P2 80×11. (i) Symplaxsofophoridium sp. from the Indreelva Member. TSGf18449e, D16-HA-80 80×18. (j) SCF problematicum from the Mara Member, N16-HA-P2 77×16. (k) Lobate or dividing acritarch, from the Indreelva Member. TSGf18449f, D16-HA-80 81×7. (l) Fragmented microfossil with a spongy envelope, Granomarginata prima from the Gibbett Hill Formation, Newfoundland. Brasier Shale A-1 87×5. Scale bar is the same for all images: 25 μm. All images are transmitted light photomicrographs.

https://doi.org/10.1017/S0016756821001096 Published online by Cambridge University Press
Table 1. A list of Ediacaran units containing the Granomarginata–Lagoenaforma association or either of the two taxa, and their approximate ages. Where this information is available, all organic-walled microfossils (OWM) are of low abundance, consistent with characterization of depauperate late Ediacaran leiosphere palynoflora (LELP) assemblage (cf. Volkova et al. 1979; Grey, 2005).

<table>
<thead>
<tr>
<th>Formation and locality</th>
<th>Likely age</th>
<th>Co-occurring taxa</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td>Upper Schwarzwand Subgroup, Namibia</td>
<td>Late Ediacaran (&lt; 548 Ma)</td>
<td>Bovinella favoeulata, “Comasphaeridium-like microfossil” similar to Granomarginata, leiosphaerids, Vendotonien sp.</td>
<td>Germs et al. (1986)</td>
</tr>
<tr>
<td>Mara Member, Dabis Formation, Namibia</td>
<td>Late Ediacaran (&gt; 548 Ma)</td>
<td>Bovinella sp., Granomarginata, Lagoenaforma coralis, Leiosphaeridia crosso, Simia annulare, Symplasmosphaeridium sp., filaments (Vendotonien)</td>
<td>This study</td>
</tr>
<tr>
<td>Malopolska Block, Poland</td>
<td>Late Ediacaran (549 ± 3 Ma)</td>
<td>Eoentophysalis sp., Granomarginata prima, leiosphaerids, Obruchevella sp., filaments (Siphonophycus)</td>
<td>Jachowicz-Zdanowska (2011)</td>
</tr>
<tr>
<td>Gibbett Hill Formation, Newfoundland</td>
<td>Late Ediacaran (&lt; 564 Ma)</td>
<td>?Granomarginata prima, leiosphaerid fragments, Lagoenaforma aff. coralis, Symplasmosphaeridium sp., serrated SCF</td>
<td>This study</td>
</tr>
<tr>
<td>Jodhpur Formation, India</td>
<td>Middle–late Ediacaran (&quot;570−542 Ma&quot;)</td>
<td>Bovinella favoeulata, Granomarginata prima, leiosphaerids, Lophophaeridiurn rurum, filaments (Siphonophycus)</td>
<td>Prasad et al. (2010)</td>
</tr>
<tr>
<td>Indreelva Member, Ståhpogieddi Formation, Arctic Norway</td>
<td>Middle–late Ediacaran (&lt; 563 Ma, postdating Gaskiers-equivalent glacial interval)</td>
<td>Granomarginata, Lagoenaforma coralis, Leiosphaeridia crosso, Leiosphaeridia jacutica, Symplasmosphaeridium sp., lobate vesicle (? Archeoeyopsis), tapering annulated microfossil</td>
<td>This study</td>
</tr>
<tr>
<td>Kotlin Formation, Estonia</td>
<td>Late Ediacaran (Kotlin regional stage)</td>
<td>&quot;Opaque acanthomorphic acracth&quot; similar to Granomarginata, Coneosphaera arctica, Simia annulare &amp; Pteropsermosimormphota sp., leiosphaerids, serrated SCF, Symplasmosphaeridium sp., prokaryotic filaments and cell aggregates</td>
<td>Arvestål &amp; Willman (2020)</td>
</tr>
</tbody>
</table>

Series 2. The new record documented here extends its distribution deeper in time as well as to a new region: Namibia.

Granomarginata is a single-celled eukaryote consisting of a central body and an uneven equatorial extension with granular surface. Its morphology resembles a phycora of prasinophyte algae (Moczydłowska, 2011). Because of its widespread palaeogeographic distribution and occurrence in sediments deposited in both shallow and deep waters, it is assumed to have been a cyst of a planktonic organism. Microfossils with distinct morphological elements (e.g. processes and envelopes) provide a useful biostratigraphic tool, and the envelope-bearing Granomarginata is one of the few non-leiosphaerid acritarchs present in low-diversity microfossil assemblages of upper Ediacaran strata, in addition to organically preserved problematica (cf. Golubkova & Raevskaya, 2005; Leonov & Ragozina, 2007; Moczydłowska et al. 2015; Slater et al. 2020). Microfossils of this material differ from more ubiquitous Proterozoic envelope-bearing taxa such as Simia (also present in the Nama Group) in their fluffy, granular envelope with an uneven outline, which is likely a result of its less resistant nature compared with the central body (Naumova, 1960; Moczydłowska, 1991). Although the material from Norway and Newfoundland is relatively poorly preserved, it possesses sufficient diagnostic features that fall into the preservational range of Granomarginata reported in younger, thermally altered sedimentary successions (e.g. Moczydłowska, 2002).

Until now, Granomarginata was considered characteristic of the lower Cambrian Lontovian regional stage of the EEP (Volkova et al. 1983; Jankauskas & Lendzion, 1992). Yet similarly to recent observations that the fossil record of some traditionally Cambrian groups such as SCF extends back into the Ediacaran (Slater et al. 2020, see also Chiglino et al. 2015), Granomarginata first occurs in older strata globally, albeit in lower abundance. In the lower Cambrian Chapel Island Formation on Newfoundland, Granomarginata precedes the first appearance of small process-bearing acritarchs characteristic of the early Cambrian Period, which was the rationale used for the establishment of the Granomarginata Zone (Palacios et al. 2018). Considering our findings and previously published data on the Ediacaran Granomarginata (Gumia, 1990; Prasad et al. 2010; Jachowicz-Zdanowska, 2011), the Granomarginata Zone could represent an extension of late Ediacaran OWM assemblages into the Cambrian. Granomarginata’s appearance on the Digerumel Peninsula is just above the beds containing the macroscopic fossil Palaeopascichnus attributed to the middle–upper Ediacaran (Fig. 2a; Jensen et al. 2018b) and below and through the horizons bearing discoidal and dickinsoniarmorph Ediacara-type macrofossils in Norway (cf. Högström et al. 2013, 2017). On Newfoundland, Granomarginata occurs in upper Ediacaran strata (Fig. 2c), in units well above formations bearing Avalon assemblage macrofossils (cf. O’Brien & King, 2004; Matthews et al. 2021). In Namibia, Granomarginata occurs in the unit below strata bearing Cloudina (cf. Germs, 1972a, 1983), and in strata overlain by a member containing the late Ediacaran Nama assemblage (Fig. 2; cf. Narbonne et al. 1997; Vickers-Rich et al. 2013; Elliot et al. 2016; Maloney et al. 2020). Rocks in these localities are not coeval, and we do not correlate them, but all three sequences represent the
post-Shuram late Ediacaran time interval (cf. Xiao et al. 2016) and offer insights about the age range of flask-shaped microfossils and *Granomarginata*.

Two *Granomarginata* morphotypes are recognized in the present material. The type with a wider equatorial extension is consistent with the diagnosis of *G. squamaecea* (Fig. 4a–d). The morphotype with a narrower extension (Fig. 4e, f) is consistent with *G. prima*. This taxon is also known from the upper Ediacaran strata of Poland (Jachowicz-Zdanowska, 2011), but it is the more pervasive morphotype in younger strata, known from the Terreneuvian deposits of the Digerumlen Peninsula (Högström et al. 2013; Palacios et al. 2020), New Brunswick (Palacios et al. 2011) and Newfoundland (Palacios et al. 2018) in Canada, from the lower-middle Cambrian of China (Yin et al. 2009), as well as from elsewhere on Baltica (Volkova et al. 1983; Jankauskas & Lendzion, 1992), the EEP (Jachowicz-Zdanowska, 2013; Szczepanik & Zylinska, 2016) and the eastern Cordillera (Rubinstein et al. 2003). In the stratigraphic correlation chart presented by Kumar & Matthy (2008), the Stähpgjeddi Formation in Norway was aligned with the Ediacaran to lowermost Cambian Kauriyla Formation of the Lesser Himalayas in India, which also contains *G. prima*. It was potentially reported from the Kuibis Subgroup in Namibia by Germs et al. (1986, fig. 6i) as a ‘Comasphaeridium-like fossil’.

*Granomarginata* is a rare component (c. ≤ 5 specimens per slide) of the leiosphaerid-dominant palynomorph assemblage (c. 50–70 leiosphaerids per sample) in the upper Ediacaran successions studied here, where it co-occurs with rare small carbonaceous problematica. Both *Granomarginata* morphotypes are more common and abundant in the Fortunian Stage, and define the *Granomarginata* Zone. Their higher abundance (> 10 specimens per slide), along with Cambrian-characteristic taxa, can be viewed as more indicative of lower Cambrian strata (e.g. Palacios et al. 2018). On the other hand, a low abundance of *Granomarginata* within a leiosphaerid-dominant assemblage, in association with flask-shaped *L. collaris*, is so far found in upper Ediacaran or transitional strata.

5.b. The life and times of the *Granomarginata–Lagoenaforma* association

The new flask-shaped microfossil *Lagoenaforma* (Fig. 5) was observed in the horizons containing Ediacaran *Granomarginata*. Flask-shaped microfossils resembling chitinozoans are common in Ordovician–Devonian strata and some non-chitinozoan flask-shaped problematica are present in Ordovician strata (e.g. Loeblich & McAdam, 1971), but have not been previously described from the Ediacaran. *L. collaris* is a minor component of leiosphaerid-dominated assemblages, but in addition to *Granomarginata* it is one of the few OWM taxa outside of dominant simple sphaeromorphs in the upper Ediacaran (LELP assemblage). As *L. collaris* is currently unknown from Cambrian units, it serves as a better representative of the late Ediacaran microbiota of the two. A low-diversity OWM assemblage with *G. prima* occurs along with ‘flask-shaped bodies’ in the lower Cambrian Withycombe Formation, UK (Rushton & Molyneux, 1990). No microfossils were illustrated in that publication, so affinities with *Lagoenaforma* could not be determined. However, the presence of other soft-bodied flask-shaped microfossils higher up in the stratigraphy on the Digerumlen Peninsula (A. Högström, pers. obs.) and in other upper Ediacaran – Cambrian units worldwide (Table 1; cf. Sabourin et al. 2003), as well as agglutinated forms (Gaucher & Sprechmann, 1999), suggests that flask-shaped OWM may be a common component of the microbiota during this transitional interval.

We found these OWM in upper Ediacaran units with a depauperate palynomorph assemblage, but their full stratigraphic range still needs to be determined. We used information on the age of the rocks hosting *Granomarginata–Lagoenaforma* to assess their age range. *Granomarginata* and *Lagoenaforma* do not co-occur with the classic acanthomorphic acritarch assemblage (ECAP/DPA) in the underlying lower Ediacaran strata in Norway (H. Agić, pers. obs.), nor have they been recognized so far in the older deposits on Newfoundland (see Hofmann et al. 1979) or elsewhere (e.g. Grey, 2005), so we view them as constituents of the late Ediacaran OWM assemblage (LELP sensu Grey, 2005). On Newfoundland, a flask-shaped microfossil was found in an assemblage hundreds of metres above the youngest occurrence of rangeomorphs in the St John’s Group that have a maximum age of 564.13 ± 0.65 Ma (U–Pb zircon data; Matthews et al. 2021). In Namibia *Granomarginata* and *Lagoenaforma* are found in the Mara Member, below all local occurrences of Ediacaran body fossils, and which records a negative δ¹³C excursion that has been interpreted as correlative with the Shuram–Wonoka CIE (cf. Grotzinger et al. 1995; Saylor et al. 1995; Narbonne et al. 1997). In Arctic Norway, these fossils appear immediately above the first occurrence of palaeopasichnids and below the first Ediacara-type fossils including discs and dickinsoniornmorphs (Högström et al. 2013, 2017; Jensen et al. 2018b), suggesting an age of 565–550 Ma based on radiisotope ages that constrain similar fossils assemblages (cf. Jensen et al. 2018b; Kolesnikov et al. 2018; Soldatenko et al. 2019). These examined units are not coeval, but their ages are mostly younger than the Shuram anomaly, the most negative carbon isotope excursion in Earth’s history and a global, synchronous event with bounding Re–Os ages of 574.0 ± 4.7 to 567.3 ± 3.0 Ma (Rooney et al. 2020). Based on these occurrences, and depending on the age of palaeopasichnids in the Indreella Member (see Jensen et al. 2018b), the *Granomarginata–Lagoenaforma* association first appeared after, or coincides with, the latest part of the Shuram excursion. It has a relatively long range to the uppermost Ediacaran, and *Granomarginata* becomes more common in the Cambrian strata.

The age uncertainty of the Norwegian strata presents two possibilities for the overall age range of the *Granomarginata–Lagoenaforma* association (Fig. 7b). The Mortensnes Formation diamictite (separated from the Indreella Member by the Lillevannet Member, Fig. 2a) is thought to be of Ediacaran age (Halverson et al. 2005). A dolomite bed 20 m below the Mortensnes diamictite on the neighbouring Varanger Peninsula contains depleted δ¹³C values (< −8‰) considered ‘a likely correlative of the Shuram–Wonoka anomaly’ (Rice et al. 2011, p. 598), and it is thought to correlate with the Shuram CIE in the upper Johnnie Formation in Death Valley, USA (Halverson et al. 2005). This suggests a younger age of the Mortensnes diamictite than the Marinoaon glaciation and it was correlated with the short-lived Ediacaran Gaskiers glaciation expressed in diamictites on Newfoundland. At the time that model was proposed, the Gaskiers was assumed to be near in age to the Wonoka (=Shuram) anomaly (cf. Halverson et al. 2005). Subsequently, the age of the Gaskiers glaciation was constrained to c. 579 Ma (Pu et al. 2016), which is older than the recent age constraints on the Shuram–Wonoka excursion based on Re–Os geochronology of strata in Oman and NW Canada (c. 574–567 Ma, Rooney et al. 2020) and estimates from astrochronology (c. 570–
This places the Shuram–Wonoka excursion after the Gaskiers glaciation. Accepting the interpretation that the negative δ13C values in the Nyborg Formation carbonates are representative of the Shuram–Wonoka anomaly, the Mortensnes diamictite could be younger than the Gaskiers and Trinity diamictites on Newfoundland, which suggests an even younger age for the base of the overlying Indreelva Member. This places it closer in age to the studied strata in Newfoundland and Namibia, and implies a narrower stratigraphic range of OWM at the end of the Ediacaran Period.

Alternatively, if the Mortensnes Formation is of Gaskiers age (Halverson et al. 2005) and therefore older than the Shuram excursion, the Granomarginata–Lagoenaforma association has approximately the same age constraint as Palaeopascichnus (Fig. 7b). This is supported by the presence of palaeopascichnids of a type around 565 Ma or younger in the Indreelva Member (Jensen et al. 2018b), just below the occurrence of OWM, which coincides with the later part of the permissible duration of the Shuram excursion. Moreover, the OWM and the palaeopascichnids occur prior to the appearance of dickinsoniamorphs (Högström et al. 2017), whose stratigraphic range is around 558–550 Ma (Narbonne et al. 2012). The older age of the Mortensnes diamictite, probably coeval with the Gaskiers and Trinity diamictites, is therefore more likely, and indicates a longer age range of Granomarginata–Lagoenaforma through late Ediacaran time.

A negative carbon isotope excursion in the Nama Group was correlated to excursions recorded in the upper Nafun (c. 550 Ma) and lower Ara groups in Oman, above the Shuram Formation (Grotzinger et al. 1995; Halverson et al. 2005). However, these depleted δ13C values in the carbonates of the Dabis Formation, including the Mara Member, have also been interpreted as heralding the end of the Shuram excursion (Hall et al. 2013; Wood et al. 2015). The excursion recorded in the Mara Member elsewhere (Kaufman et al. 1991; Wood et al. 2015) is not fully expressed in the sampled section, possibly because the Pockenbank area was on a palaeo-high compared with that of other localities that record the Shuram anomaly in full (see Vickers-Rich et al. 2016). Additional micropalaeontological investigation is needed to evaluate the extent of the association’s range through the lower Nama Group and in relation to its chemostratigraphy.

Throughout the late Ediacaran interval, both Granomarginata and Lagoenaforma are rare in comparison to leiosphaerid and filamentous microfossils, but still more morphologically distinct than most other OWM in the upper Ediacaran strata. The association also co-occurs with the cocoid aggregate structure Bavlinella sp. (Fig. 6h), which is relatively common in Neoproterozoic strata (cf. Vidal, 1976) and was previously recovered from the Ediacaran strata of Namibia by Germs et al. (1986). Smooth-walled OWM (leiosphaerids; Fig. 6a, b, d) are the most abundant component of the examined assemblages, consistent with the idea that the late Ediacaran microbiota was generally of low diversity and dominated by simple leiosphaerids (Moczydłowska, 1991; Grey, 2005). Lophosphaeridium is another OWM best known from Cambrian strata that was also reported from the upper Ediacaran Frecheirinha Formation (Chiglino et al. 2015) and
Maricá and Bom Jardin groups in Brazil (Lehn et al. 2019). This taxon was not found in the present material, so it may not have been distributed globally or it may have been restricted to a specific environment, and more work is needed to assess its distribution at this time. Regardless, both Lophospheraeidi um and Granomarginata first appeared during the rise of macroscopic Ediacara-type biota, and have subsequently diversified and became more prominent components of OWM assemblages in the Cambrian strata (e.g. Moczydlowska, 1991; Palacios et al. 2018).

Because of the presence of taxa and fossil groups that 'cross' the Ediacaran–Cambrian boundary, the composition of whole assemblages may also be relevant for the OWM biostratigraphy of the Ediacaran–Cambrian transition. A leiosphaerid-dominant assemblage with Lagoenaforma in association with Granomarginata is present in multiple palaeogeographic areas and, pending further studies, has potential to be broadly used as one of the indicators of the upper series Ediacaran. However, this association may also reflect a specific environmental control.

5.c. Palaeoenvironmental implications

Our new data show that Granomarginata and Lagoenaforma are relatively rare components of the late Ediacaran microbiota, but were present on several palaeocontinents (Fig. 7a; Table 1). The studied strata in Norway, Newfoundland and Namibia are not coeval, but can be viewed as part of the upper series Ediacaran (cf. Xiao et al. 2016). Considering the palaeogeographic reconstruction for this time, the Granomarginata–Lagoenaforma association was widely dispersed (Fig. 7a), and possibly an assemblage of cosmopolitan taxa. The association could be representative of taxa occupying a specific type of environment. All strata in which this assemblage occurs (including the upper Ediacaran rocks bearing Granomarginata in India, Poland and Baltica; Prasad et al. 2010; Jachowicz-Zdanowska, 2011; Arvestål & Willman, 2020), represent a marine shallow-water to marginal shelf environment. Leiosphaerids are usually highly abundant in nearshore, shallow-water environments (e.g. Li et al. 2004). They comprise most of the OWM assemblage containing Granomarginata and Lagoenaforma, so this is further indication of a shallow-water setting.

Acanthomorphic OWM characteristic of ECAP/DPA do not occur in the studied strata, although rare cases of late Ediacaran acanthomorphs are documented in Mongolia (Anderson et al., 2017, 2019) and Siberia (Grazhdankin et al. 2020). These assemblages are an exception among the depauperate OWM assemblages prevalent at this time (Grey, 2005; Leonov & Ragozina, 2007). While the pre-Shuram ECAP assemblages are generally diverse (e.g. 54 taxa in the Doushantu Formation; Xiao et al. 2014), the LELP assemblages tend to contain fewer taxa (e.g. 16 in the Lyamtsa Formation, White Sea region; Leonov & Ragozina, 2007), many of which are bacterial. The exceptionally preserved microfossils from the Khenes Formation in Mongolia exhibit Doushantu-style preservation (Anderson et al. 2017), similar to ECAP microbiota from phosphorites of the lower Ediacaran Doushantu Formation in China (e.g. Xiao et al. 2014). The Khenes assemblage is preserved in phoshatic grainstones, within a sediment-starved, condensed carbonate succession. The acid-extracted acanthomorphs from the Oppokun Formation in Siberia occur in a thick succession of mudstones (Grazhdankin et al. 2020), probably deposited in a low-energy environment. These occurrences in different depositional environments may result in different assemblages: nearshore shallow marine in the case of the Granomarginata–Lagoenaforma association and depauperate leiosphaerid assemblage (LELP) recognized by Grey (2005), or low-energy environments in the case of ECAP. The overall dearth of microfossils across the Ediacaran–Cambrian transition could also be a result of the lack of sampling for palynological analyses, or a depositional hiatus. Many relevant successions consist of mainly unsuitable lithologies for OWM preservation (especially in Australia; Grey, 2005), although this is not the case on EEP and Baltica. The dearth of OWM could also relate to the Kotlinian Crisis: a drop in diversity of soft-bodied taxa near the increase of bioturbation and expansions of reef-builders (Kolesnikov et al. 2015).

Some prasinophyte-like OWM (in addition to Granomarginata, e.g. Tasmanites and Pterosperma-like morphotypes) persisted through the Ediacaran–Cambrian transition, and it was suggested that perhaps these organisms played a role as primary producers in sustaining the metazoan ecosystem during this transitional interval (Moczydlowska, 2011). This is difficult to reconcile with biomarker evidence for bacterially dominated primary production on Baltica and the EEP in the upper Ediacaran strata (Pehr et al. 2018). Prasinophytes are generally successful in low diversities of other phytoplankton taxa and in an aftermath of crises, which labels them disaster-taxe (e.g. van de Schoubrugge et al. 2007). A community of such disaster-taxe and potential mixotrophs (flask-shaped microfossils) is therefore a likely response of eukaryotic microbiota to ecosystem perturbations (cf. Kolesnikov et al. 2015; Wood et al. 2019) through the late Ediacaran Period.

6. Conclusions

The organic-walled microfossil Granomarginata, otherwise a constituent of lower Cambrian acritarch assemblages, was recovered from middle–upper Ediacaran strata, in addition to a new taxon Lagoenaforma collaris gen. et sp. nov. New locations include three palaeocontinents: Avalonia (Newfoundland), Baltica (Norway) and adjacent to the Kalahari Craton (Namibia). While Granomarginata survived into and became more prominent in the Cambrian, Lagoenaforma is so far known only from the Ediacaran, although other neck-bearing forms occur in the lowermost Cambrian strata in Norway. Problematic microfossils in other Ediacaran units resembling Granomarginata are reviewed in this study; the taxon’s occurrence was additionally documented elsewhere on Baltica, the Indian palaeocontinent and the Malopolska Block of Poland (Table 1). The stratigraphic range of Granomarginata is therefore extended further back in time, which places it into the so-called late Ediacaran leiosphaerid palynoflora (LELP; sensu Grey, 2005), a depauperate assemblage of predominantly sphaeromorph and envelope-bearing organic-walled microfossils. Our records from three palaeocontinents and previous reports show that both taxa were geographically widespread by late Ediacaran time. Their occurrence deeper in the stratigraphy suggests a protracted transition into Cambrian-like assemblages.

Co-occurring taxa include prokaryotic OWM and organic problematica (Table 1). Granomarginata and flask-shaped microfossils occur in strata that mostly postdate the Shuram–Wonoka excursion and so far have not been recovered from lower Ediacaran assemblages (cf. Hofmann et al. 1979; Grey, 2005; Agic et al. 2019). Based on these occurrences in post-Gaskiers and post-Shuram rocks, the age range of the Granomarginata–Lagoenaforma association is broadly late Ediacaran.
Together, the record presented here along with other reports on late Ediacaran microfossils support the conclusion that some OWM and SCF survived into the Phanerozoic Eon with their abundance increasing during the Cambrian Period. The LELP assemblage is indeed dominated by leiosphaerids, but contains more taxa than previously recorded, even outside the few Doushantuo–Prtatataka acritarch assemblages that persisted into the upper Ediacaran. Although this record is rather limited, it calls for a more thorough palynological investigation of middle–upper Ediacaran strata. Globally, few units have been examined in detail (with the exception of Russia and Ukraine), so perhaps the diversity of late Ediacaran protistan microfossils is underestimated. Additional OWM records in such little-studied deposits could not only aid in biostratigraphic endeavours, but also help constrain the timing of the turnover of late Neoproterozoic microscopic eukaryotes, and the onset of the microbiota characteristic of the early Phanerozoic Eon.

7. Systematic palaeontology

Genus Granomarginata Naumova (1960)

Type species. Granomarginata prima Naumova (1960), p. 114 described from the lower Cambrian 'Blue Clay' (=Lontova Formation) of Estonia.

Remarks. Specimens of Granomarginata in the present material resemble Ostiumsphecididium complitum (Vorob’eva et al. 2009, figs. 14.1, 14.2) from the upper Neoproterozoic strata on the East European Platform, found in association with large spinose OWM (DPA/ECAP). Both taxa have a darker central body with a flabby extension, yet the vesicle of (DPA/ECAP). Both taxa have a darker central body with a fluffy envelope—bearing Pterospermopsis morpha. A disphaeromorph, Pterospermopsis morpha is a sphere–within–sphere with a well outlined inner vesicle and a robust outer envelope (e.g. Jankauskas et al. 1989, pl. 3, figs 3–8; Agić et al. 2017, fig. 10a–c). The inner vesicle is not always centrally located within the envelope, as is the case in Simia or Granomarginata. Pterospermopsis morpha is quite rare in Ediacaran strata relative to other OWM taxa (Grey, 2005), as well as compared with its abundance in pre-Cryogenian fossiliferous units (H. Agić, pers. obs.).

Granomarginata prima Naumova (1960)

Figure 4e, f

Synonymy. cf. 1986 ‘Comasphaeridium–like fossil’; Germs et al., p. 56, fig. 5i.

1990 Granomarginata sp.; Gunia, p. 109, pl. 1, figs 10, 11.

2010 Granomarginata prima; Prasad et al., p. 420, pl. 1, fig. 6.

2011 Granomarginata prima; Jachowicz–Zdanowska, p. 91, fig. 4f.

See additional synonymy of Cambrian specimens by Palacios et al. (2018).

Material. Two specimens (D16-80 84.5×18 and D16-80 81×14) from the Indreelva Member, Stáhpogieddi Formation, Vestertana Group in Norway. One complete specimen and one hemisphere fragment (N16-HA-3 79×16) from the Mara Member, Dabis Formation, Nama Group, Pockenbank in Namibia. A fragment of a vesicle with a spongy envelope from the Gibbett Hill Formation, Signal Hill Group on Avalon Peninsula in Newfoundland (Brasier Shale A-1 87×5).

Description. Round to oval, discoid vesicles with central body that is surrounded by a narrow, membrane-like, spongy extension. The extension rim on our specimens is uniform in width, but it seems less resistant than the central body, so it is occasionally fragmentary or appears etched and uneven.

Dimensions. Vesicle diameter range observed in G. prima is 24–40 μm (cf. Moczydłowska, 1991). In the present material, the overall diameter of the microfossil ranges over 31–39 μm, n = 4, mean (X) = 35.5 μm, standard deviation (σ) = 4.8 μm.

Remarks. G. prima differs from G. squamacea in a narrower rim. There is no prior known occurrence of Granomarginata from Namibia. However, Germs et al. (1986) have documented an acritarch specimen strongly resembling G. prima, identified as ‘Comasphaeridium–like fossil’ (Germs et al. 1986, fig. 6i) from the upper Kuibis subgroup. Although the specimen is poorly preserved, and its features are difficult to discern in the black-and-white photomicrograph, it appears to bear a narrow spongy rim characteristic of G. prima. Poorly preserved specimens of Granomarginata may superficially resemble acanthomorphic acritarchs with thin processes (cf. Spina et al. 2020, pl. 1 figs 6–8). Specimens of G. prima from upper Ediacaran strata represent this species’ oldest known occurrence to date, but they are very rare in Ediacaran units, in comparison to the taxon’s ubiquity in the Cambrian strata. It is a more common component of the Granomarginata Zone and Asteridium tornatum–Comasphaeridium velutum Zone in the Terreneuvian Series (Fortunian) of lower Cambrian strata, as well as in the Volkovia dentifera–Lepina plana and Skiagia ornata–Fimbrioglomerella membranacea zones in Cambrian Series 2 (Palacios et al. 2018, 2020). Examples of Granomarginata with a...
darker central body are common in the thermally altered rocks, for example in the Sávvoare/Grannagjukku formations in Sweden (Moczydłowska, 2002) and higher up in the stratigraphy on the Digerenlumen Peninsula (Mannadrevsela Member; Högström et al., 2013, fig. 6C), as well as in some strata with lower thermal alteration such as the File Haidar Formation in Sweden (Eklund, 1990).

**Occurrence.** In Ediacaran-age deposits, *Granomarginata prima* occurs in the following units: Indreelva Member, Stáhpogieddi Formation, Vestertana Group, Norway; Dabis Formation, Nama Group, Namibia; Jodhpur Formation, Marwar Supergroup, India (Prasad et al. 2010); boreholes from the Malopolska block adjacent to East European Platform, Poland (Jachowicz-Zdanowska, 2011); and potentially Gibbett Hill Formation, Signal Hill Group, Newfoundland. For a list of Cambrian occurrences of *G. prima*, see work by Moczydłowska (1991, 2011) and Palacios et al. (2018). *G. prima* and organic problematica are found also in the Cambrian strata on the Digermulen Peninsula (Manndrapselva Member; Högström et al., 2010); boreholes from the Maipo Napal block highlighted the strata containing upper Ediacaran macrofossils in Namibia. *Palaeopascichnus delicatus* is in the equatorial part. The extension is thin and of varying breadth; it often appears uneven in outline or etched. The first appearance of *G. prima* is in the upper Ediacaran strata above the first appearance of *Palaeopascichnus delicatus* estimated at < 565 Ma (cf. Jensen et al. 2018). Other Ediacaran occurrences include an additional record from Baltica – *Granomarginata*-like acritarch from the Kotlin Formation in Estonia (Arvestål & Willman, 2020) – as well as the material documented here from the Dabis Formation, Nama Group in Namibia. For a compilation of global Cambrian occurrences, we refer to Moczydłowska (1991, 2011).

**Stratigraphic range.** The first appearance of *G. prima* is in the upper Ediacaran strata above the first appearance of *Palaeopascichnus delicatus* and discoidal macrofossils in Norway, and below the strata containing upper Ediacaran macrofossils in Namibia. The taxon ranges to the Mialingian Series (Moczydłowska, 1991).

*Granomarginata squamacea* Volkova (1968)  
**Figure 4a–d**

**Synonymy.** cf. 2020 ‘unknown c’; Arvestål & Willman, fig. 12d.  
See additional synonymy of Cambrian occurrences by Moczydłowska (2011).

**Material.** Three specimens and three fragments (D18-HA-20 81x6, D16-HA-80 87x19, D16-HA-80 85x21) from near the base of the Indreelva Member, Stáhpogieddi Formation (Vestertana Group), exposed on the Digerenlumen Peninsula, Norway. Two specimens and three fragments (N16-HA-P2 82x13, N16-HA-P3 81x9) from the Mara Member, Dabis Formation, Nama Group, from Farm Pockenbank, southern Namibia.

**Description.** Circular to oval vesicles consisting of a central body surrounded by a wide, spongy, membranous extension in the equatorial part. The extension is thin and of varying breadth; it often appears uneven in outline or etched.

**Dimensions.** Vesicle diameter of *G. squamacea* in the material reported here ranges over 32–58 μm, \( n = 9 \), \( \Sigma = 45.7 \) μm, \( \sigma = 8.2 \) μm, marginally larger than the reported size range for this taxon of 20–55 μm by Moczydłowska (2011). Central body diameter is 25–32 μm.

**Remarks.** Unlike *G. prima*, the extension in *G. squamacea* is often creased. Moczydłowska (1991, p. 57) noted that the spongy part of *G. squamacea* “appears as irregular ‘filaments’ on the outline of the equatorial zone”. In a few poorly preserved specimens this may lead to their erroneous identification as an acanthomorph taxon with dense thin processes, for example, *Comasphaeridium*. This filamentous appearance of the extension was probably obtained as the vesicle underwent post-depositional compression. Specimens of *G. squamacea* in this material differ from other Proterozoic envelope-bearing taxa such as *Simia* and *Pterospermopsismorpha* in a membranous, spongy extension and fluffy wall (Moczydłowska, 1991), as mentioned above. The distinction between the two taxa was also illustrated by Moczydłowska (2002, fig. 9.3, 9.4). *G. squamacea* with an opaque central body is also known from the thermally altered Cambrian strata of the Swedish Caledonides (Moczydłowska, 2002, fig. 9.4). Such an appearance is then not unexpected within the Indreelva Member, where the sediments have experienced tectono-metamorphic deformation related to the late Scandian Orogeny, and have a postmature overprint of 200–250 °C (Meinhold et al. 2019b). Some Neoproterozoic specimens of *G. squamacea* (Pyatiletov, 1988) were subsequently dismissed as globular kerogen particles (Vidal et al. 1995). *G. squamacea* is rare compared with leiosphaerids or filamentous organic-walled microfossils from the same samples.

**Occurrence.** The first appearance of *Granomarginata squamacea* to date is in the Ediacaran Stáhpogieddi Formation, Vestertana Group (Arctic Norway), above the first occurrence of *Palaeopascichnus delicatus* estimated at < 565 Ma (cf. Jensen et al. 2018). Other Ediacaran occurrences include an additional record from Baltica – *Granomarginata*-like acritarch from the Kotlin Formation in Estonia (Arvestål & Willman, 2020) – as well as the material documented here from the Dabis Formation, Nama Group in Namibia. For a compilation of global Cambrian occurrences, we refer to Moczydłowska (1991, 2011).

**Stratigraphic range.** The range of *G. squamacea* is hereby extended lower in the stratigraphy, from above the deposits of the Ediacaran glaciation and the first appearance of palaeopascich- nids in Norway, and below the unit containing macrofossils of the Nama assemblage in Namibia.

**Genus Lagoenaforma gen. nov.**

**Type species.** *Lagoenaforma collaris* gen. et sp. nov.

**Etymology.** From the Latin lagoena, -ae, f. (loaned from the Greek λαγηνος) meaning pitcher or flask, and forma, -ae, f., meaning shape, describing the microfossil’s resemblance to a wine pitcher. Pliny the Younger (Mynors, 1963) refers to his hunting flask as lagena/laguncula.

**Description.** As for type species.

*Lagoenaforma collaris* gen. et sp. nov.  
**Figure 5a–c**

**Synonymy.** cf. 1988 ‘chitinozoan-like microfossil, Form II’; Zang, pl. 16, figs A, B.  
1989 *Germinosphaera guttaformis*; Jankauskas et al., pl. 47, fig. 7.  
2003 *Chitinozoa-like microfossils*; Sabouri et al., pl. 3, fig. 10.

**Etymology.** From Latin collum, -i, m. meaning neck, in reference to the neck-like protrusion from the elongate vesicle.

https://doi.org/10.1017/S0016756821001096 Published online by Cambridge University Press
Holotype. TSG18449c 78×15, sample D16-HA-80 (Fig. 5a) from the Ediacaran Indrelva Member, Ståhpogieddi Formation, Vestertana Group in Norway.

Material. Ten specimens in total. Four specimens (D16-HA-80 78×15, D16-HA-80 83×4, D16-HA-53 85×9, D16-HA-53 79×18) well to moderately well preserved from the Indrelva Member, Ståhpogieddi Formation (Vestertana Group) on Digerumlen Peninsula, Arctic Norway. Three specimens (N16-HA-P2 76×7, N16-HA-P2 77×5.5, N16-HA-P2 79×11) from the Mara Member, Dabis Formation, Nama Group, on Farm Pockenbank, southern Namibia.

Diagnosis. Oval to elongate vesicle with a neck-like protrusion. The neck is open distally and terminates by widening outwards; it never tapers. The neck is up to one third of the overall vesicle length. Wall texture smooth to chagrinate.

Dimensions. The length of the vesicle including the ‘neck’ is 67–94 μm (σ = 78 μm, σ = 10.7 μm, n = 9). The opening of the ‘neck’ ranges over 15–32 μm. The neck width is 12–30 μm, except the outlier specimen from the Gibbett Hill Formation which possesses a 4-μm-wide ‘neck’.

Remarks. L. collaris exhibits no ornamentation or sculpture, but its wall texture can be smooth (Fig. 5a) or fluffy (Fig. 5b, c), which is likely a preservational feature. The Newfoundland specimen is opaque akin to other microfossils from the Gibbett Hill Formation (e.g. Fig. 6c). This is common in OWM from units that have undergone a higher degree of thermal alteration (Spina et al. 2018), but it can also result from accelerated degradation in oxygenated environments (Schiffbauer et al. 2012). The Newfoundland specimen has a narrower ‘neck’ compared with other specimens of L. collaris (4 μm in width), but the widening outwards at the tip indicates that the ‘neck’ structure is not a process, but likely an open-ended protrusion.

Jankauskas et al. (1989) erected a new species of a long-ranging Precambrian taxon Germinosphaera that includes one flask-shaped morphotype: G. guttaformis from the upper Riphean (=Tonian–Cryogenian) of Siberia. Only one specimen in their material has an elongate, flask-shaped main vesicle and a thick single process, truncated at the tip, whereas the rest possess a thick, circular vesicle 80–60 μm in diameter (Jankauskas et al. pl. 47, figs 7, 8). G. guttaformis specimen on plate 47, figure 8 has a narrower process, more similar to the narrow ‘neck’ in the Gibbett Hill specimen described here, but its vesicle is still bigger and more rounded than that of L. collaris. Although the rest of G. guttaformis material described by Jankauskas et al. (1989) is relatively consistent, a single elongate specimen (pl. 47, fig. 7) is unlike other members of this genus; both the original and emended diagnoses for Germinosphaera imply a circular vesicle (Mikhailova, 1986; Butterfield et al. 1994). That morphotype therefore does not belong to Germinosphaera, and we do not include our similar specimens into this genus. Willman & Moczydłowska (2011, pl. 7, fig. 7) illustrated a flask-like microfossil interpreted as a fragmented cyanobacterial sheet from the upper Dey Dey Mudstone in the Officer Basin, Australia, Tanarium-bearing beds. That morphotype differs from L. collaris in its longer and straighter ‘neck’.

Some chitinozoan-like microfossils from several sections of the upper Ediacaran Kahar Formation in northern Iran (Sabouri et al. 2003, pl. 3, fig. 10) are comparable to L. collaris. Similar ‘chitinozoan-like microfossils’ were also reported from the Liulaobei Formation, Huainan Group in China (Zang, 1988), now understood to be Tonian in age (see Tang et al. 2013). An outlier among those microfossils, called ‘Form II’ (pl. 16, figs a, b), resembles L. collaris in shape and size. Zang (1988) noted that distribution of ‘chitinozoan-like’ microfossils declined from deep to shallow water, which is in contrast to present material where L. collaris occurs in shallow-water environments. The relationship of L. collaris to these Tonian OWM is unclear. Additional soft-bodied forms similar to L. collaris from the Proterozoic Vindhyan Supergroup of India (Maithy & Babu, 1989, pl. 1) were attributed to chitinozoans, including Melanocryllium. However, those microfossils lack diagnostic characteristics of Melanocryllium like a well-defined aperture and a curved neck (Bloeser, 1985). Superficially similar morphology to L. collaris is seen in mineralized vase-shaped microfossils (VSM) with long necks from the Neoproterozoic Urucum Formation in Brazil (Morais et al. 2017, figs 6.7–6.9), interpreted as testate amoebae. VSMs with a mineralized or organic wall coated by minerals are mostly found in upper Tonian organic-rich shales (Porter et al. 2003). Chai et al. (2020) reported an uncharacteristically young occurrence of VSM from the late Ediacaran Dengying Formation in China. In contrast to Lagoenaforma, those are permineralized in three dimensions, and differ in that they have a shorter and narrower ‘neck’.

The flask-shaped morphology mostly resembles chitinozoans, organic-walled marine microfossils common in Ordovician–Devonian strata. Few flask-shaped, neck-bearing, organic taxa are known from the Proterozoic and Cambrian strata (e.g. Yin, 1980), and there is a rare Cambrian Stage 5 occurrence of chitinozoans (Shen et al. 2013); however, due to the simple morphology of L. collaris, further comparisons are impractical. Lagoenaforma is also similar to Ordovician flask-like OWM Arenoricanium (Deunn, 1955). They differ in size and shape of the neck structure, which is wider and shorter in L. collaris, and the texture of its organic wall, which is thinner and smoother among Arenoricanium species. The difference in the vesicle wall could potentially be attributed to preservation as the Ediacaran fossils studied here are not as exquisitely preserved as the Ordovician material. Nevertheless, Arenoricanium has a well defined stratigraphic range (Loeblich & MacAdam, 1971) and lacks a Cambrian record, so such a significant time gap makes it less likely that these fossils represent the same or a related organism. L. collaris also differs from the Cambrian acanthomorphic acritarch Volkovia dentifera (Downie, 1982) by its overall larger size, and a shorter and wider protrusion instead of the narrow, single process of Volkovia. The distal tip of the process in Volkovia is pointed and closed (cf. Moczydłowska, 1991), whereas the neck in L. collaris is open-ended and slightly widens outwards. The possibility that the protrusion in L. collaris is truncated and could therefore represent a Volkovia with a broken-off process (or another single-processed OWM such as Alliumella baltica Umnova & Vanderflit, 1971) is dismissed because the L. collaris ‘neck’ terminates with a widening end (Fig. 5).

A single microfossil from the Mannndraselva Member (Fig. 5d) possesses a neck-like structure akin to L. collaris, but its main vesicle is rounded and its ‘neck’ is shorter, which is more similar to Sinianella uniplicata (Yin, 1980). The Mannndraselva Member includes additional neck-bearing OWM but with a more rounded vesicle and much longer neck structures (Palacios et al. 2017; A. Högbom, pers. obs.).

L. collaris shares the morphology of a flask-shaped body plan with a variety of living non-testate protists. A neck-like opening
Late Ediacaran occurrences of the organic-walled microfossils

is commonly an indicator of a mixotrophic lifestyle. Some protozoan ciliates possess a variety of oral bulges used in feeding (e.g. *Enchelyodon longikineta*, Şenler & Yıldız, 2003, fig. 2), similar to the ‘neck’ of *L. collaris*. *Vasicola ciliata* (Taylor & Sanders, 2010; fig. 3.22.O) has a soft-bodied, chitinous lorica (protective outer covering) in the shape of a pitcher, and the chitinous composition would increase its preservation potential. However, apart from these morphological similarities, the affinity of *L. collaris* is unclear.

**Occurrence.** The taxon appears in the Ediacaran shales and siltstones of the Indreelva Member, Stáhpogieddi Formation, Vestertana Group in Norway; Marä Member, Dabis Formation, Nama Group in Namibia; and the Gibbett Hill Formation, Signal Hill Group in Newfoundland.

**Stratigraphic range.** Upper Ediacaran.

**Material.** One specimen and one fragment (*Brasier Shale A*-1 89×7, 91×11,) from the Gibbett Hill Formation, Signal Hill Group on Avalon Peninsula, Newfoundland.

**Description.** Oval to elongate vesicles with a neck-like protrusion. The base of the neck is slightly wider. The necks are open distally and terminate by widening outwards; they never taper. The necks are up to one third of the overall vesicle length. Wall texture smooth to chagrinate.

**Dimensions.** The length of the vesicle including the ‘neck’ is 87 μm. The ‘neck’ is 5 μm wide and 7 μm wide at the tip.

**Remarks.** This flask-shaped OWM differs from *Lagoenaforma collaris* in a longer and narrower ‘neck’ structure. It is similar to, but half the size of, some rare, enigmatic, flask-shape structures from the Wallara 1 drill hole, lower Ediacaran Pertatataka Formation in Australia (Grey, 2005, fig. 27c).

**Unnamed Form A**

**Figure 5c**

**Material.** One specimen (TSGf18451a 89×23, sample D16-HA-77) from the Manndrapselva Member, Ståhpogieddi Formation, Vestertana Group on the Digermulen peninsula, Arctic Norway.

**Description.** Rounded vesicle with short and wide neck-like protrusions, flaring outwards. The vesicle wall has bulbous sculpture.

**Remarks.** This specimen resembles *Sinianella uniplicata* (Yin, 1980), but it differs from it in having a bulbous wall sculpture. It is unclear from observing a single specimen if the body is composed of smaller cells or if those are a part of the wall sculpture. A similar microfossil with an opaque wall and a wide-based, neck-like protrusion from the middle–upper Santa Bárbara Group, Camaquá Basin in Brazil was assigned to *Germinosphaera* sp. (Lehn et al. 2019, fig. 3). The Brazilian specimen bears a strong similarity to a truncated *Germinosphaera*, but also possesses a wider process base compared with members of this genus (cf. Butterfield et al. 1994), and appears as a ‘neck’ structure terminating in an opening. Unnamed Form A differs only slightly from the Camaquá Basin specimen in a widening-outwards ‘neck’. Further micropalaeontological examination of middle–upper Ediacaran strata worldwide will show the frequency of this morphotype. OWM with short, neck-like protrusions are not uncommon in the Precambrian though; such morphologies were also reported from the Mesoproterozoic strata of northern China (Agić et al. 2017, fig. 13d, e), and the genus *Sinianella* from Tonian–lower Cambrian strata (Zang, 1988).

Similar OWM occur in the Ediacaran Kahar Formation in Iran as *Melanocyrillium* (=*Melanocyrillium*), alongside late Ediacaran SCF *Cochleatina* (Sabouri et al. 2003, pl. 3, figs 7–9). However, *Melanocyrillium* is a Tonian VSM taxon that differs from these chitinozoan-like microfossils with a curved neck and well defined aperture, as well as in the mode of preservation (cf. Bloeser, 1985).

**Unnamed Form B**

**Figure 6c**

**Material.** Two specimens (*Brasier Shale A*-1 91×11, ‘Brasier Shale A*-1 90×13) in the Gibbett Hill Formation, Signal Hill Group, Ferryland on the Avalon Peninsula, Newfoundland.

**Description.** Elongate and straight, organically preserved microfossil with short lateral protrusions. Both specimens are truncated, up to 160 μm in length and 32 μm in width. Individual protrusions are broken distally, and up to 7 μm wide.

**Remarks.** Problematic SCF are common in uppermost Ediacaran and lower Cambrian units worldwide (Moczydlowska et al. 2015; Slater et al. 2020). Previously, the youngest occurrence of SCF in Newfoundland was documented from the Random Formation (Cambrian Stage 2) on Burin Peninsula (Palacios et al. 2018).

This form co-occurs with leiosphaerids and fragments of *Granomarginata prima* in the Gibbett Hill Formation. Similar forms have been observed in the Ediacaran–Cambrian transition strata on the Digermulen Peninsula in Norway (A. Högström, pers. obs.). Arvestål & Willman (2020, fig. 12K, p. 26) documented a hooked microfossil with lateral serrations from the Ediacaran of Estonia, ‘possibly related to *Ceratophyton*’. In contrast, the Gibbett Hill microfossils are straight and have more defined and spread out lateral protrusions.

A high degree of coalification is evident in the dark colour of Gibbett Hill Formation microfossils (including leiosphaerids), corresponding to TAI = 4.

**Unnamed Form C**

**Figure 6e**

**Material.** One specimen (TSGf18450b 85×9, D16-HA-53) in the Indreelva Member, Ståhpogieddi Formation, Digermulen Peninsula, Norway.

**Description.** Elongate and conical vesicle. One end is tapering outwards, closed and blunt. The other end is nearly twice as wide and terminates in a wide opening. The vesicle appears creased, almost annulated.

**Remarks.** This microfossil shares an ovoidal shape and a similar polar opening to the Ediacaran–Cambrian taxon *Teophipolia lacera* Kirjanov in Volkova et al. 1979 (e.g. Jankauskas et al. 1989, pl. 54, fig. 5); however, Unnamed Form C is smaller and narrower, with a faintly annulated vesicle. Similar microfossils also occur in the Cambrian Breidvika Formation, upper Vestertana Group on
the Digerumlen Peninsula (A. Högström, pers. obs.). This form is also strongly similar to Navifusa crassa (Sin & Liu, 1978), a rod-like vesicle with rounded ends and occasionally a distal opening on one end (cf. Zang, 1988, pl. 40, fig. H). However, even though specimens of N. crassa with a crumpled or faintly annulated wall have been documented (Zang, 1988), the original description of this taxon implies a smooth surface texture and a spongy wall. This contrasts with the delicate annulation in Unnamed Form C, so we consider it a separate entity.

Acknowledgements. This research was supported by the Swedish Research Council (Vetenskapsrådet) international postdoctoral grant (VR2016-06810) to H. Agić. Fieldwork in Arctic Norway was part of an expedition by the Digerumlen Early Life Research Group (DELRG) funded by the Norwegian Research Council (grant no. 231103) to A. Högström. S. Jensen acknowledges funding from Ministerio de Economía, Industria y Competitividad (grant no. CGL-2017-87631-P). Material from Namibia was collected during the 35th IGCP pre-conference field workshop to the Nama Group of southern Namibia, sponsored by IGCP 587 project ‘Identity, Facies and Time: The Ediacaran (Vendian) Puzzle’ and the ICS Subcommission on Ediacaran Stratigraphy, organized by P. Vickers-Rich, G. Narbonne, M. Laffalm, S. Darroch, A.J. Kaufman and L. Kriesfeld. In addition to workshop attendees, they are thanked for a delightful journey and engaging discussions in the field. Thanks also to C. Schneider, then Director, and staff at the Namibian Geological Survey for facilitating the IGCP 587 field conference, and to the owners of Farm Aar and Farm Pockenbank, B. Boehm Enni and L. Gesart, for allowing access to their lands. We are also grateful to T. Palacios (University of Extremadura) and K. Grey (Geological Survey of Western Australia) who provided valuable feedback on an earlier draft, and thank three anonymous reviewers for their constructive comments.

References


Germs GB (1972b) The stratigraphy and palaeontology of the lower Nama Group, South West Africa. Precambrian Research Unit, University of Cape Town, Bulletin 12, 1–250.


https://doi.org/10.1017/S0016756821001096 Published online by Cambridge University Press
Late Ediacaran occurrences of the organic-walled microfossils


southern Namibia. Palaeogeography, Palaeoclimatology, Palaeoecology 556, 109884.


Late Ediacaran occurrences of the organic-walled microfossils


Slater BJ and Willman S (2019) Early Cambrian small carbonaceous fossils (SCFs) from an impact crater in western Finland. Lithos 320, 570–82.


